

Dry season habitat and patch selection by African buffalo herds: test of a new home range estimator

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ABSTRACT

Traditional home range estimators, the minimum convex polygon and kernel methods, provide poor resolution of within-range space-use. Using multi-year locational data of buffalo herds, we investigate buffalo selection at two scales—habitat-level and patch-level selection—following the Neu method and the new home range model, k nearest-neighbour convex-hull (k-NNCH). The k-NNCH method implicitly delineates patches of high-use and no-use, thereby allowing for easy comparisons. From comparisons of four grass species preference indices, mean grass height and a river density index between patch differences were investigated. Results of a hierarchical general linear model show that the river density index and grass preference index-3 were significant contributors to our model ($R^2=0.664$, $p<0.001$; $R^2=0.407$, $p=0.01$, respectively). Our results provide ecological insight into the selection processes of the study populations of buffalo herds and, additionally, validate the utility of the k-NNCH in providing an ecologically meaningful representation of internal range resource use.

Key words: African buffalo, *Syncerus caffer*, Kruger National Park, home range, minimum convex polygon, kernel methods, k nearest-neighbour convex-hull

INTRODUCTION

For decades, home range studies and analyses have been conducted on a diverse assemblage of vertebrate species. Over the years the mathematical methods employed have changed, often increasing in complexity (Mohr, 1947; Jenrich & Turner, 1969; Worton, 1989; Blackwell, 1997; Getz & Wilmers, 2004). The increased complexity of home range models has often provided a more accurate and higher resolution depiction of within-range space-use, as the assumption underlying all home range estimators is that the coverage produced is an ecologically meaningful unit.

The most basic method, in terms of implementation and internal range resolution, is the minimum convex polygon (MCP; Mohr, 1947). Although the shortcomings of this method are widely recognized, such as inclusion of known areas of non-use and extreme sample size bias (Worton, 1987), the ease with which it is applied likely accounts for its continual use (Ratcliffe & Crowe, 2001; Newton-Fisher, 2003; Te Wong, Servheen & Ambu, 2004). Other home range estimators that have received little attention in the literature are based upon assumptions of bivariate normality (Jenrich & Turner, 1969; Metzgar, 1973; Macdonald, Ball & Hough, 1980; in Worton, 1987). Such models based on normal distributions produce circular home ranges (Worton, 1987), which inadequately describes most real datasets.

Presently, a vast majority of home range studies implement the kernel models, fixed and adaptive (Worton 1989; Ratcliffe & Crowe, 2001; Newton-Fisher, 2003; Te Wong, Servheen & Ambu, 2004). The kernel method's popularity appears largely due to its proven ability to outperform its precursors in Monte Carlo simulations (Worton, 1995; Seaman & Powell, 1996) and provision of greater internal range resolution through an integrated utilization distribution (UD) function. However, the blanket UDs calculated by the kernel methods often overlap or cover areas of known non-use (Getz & Wilmers, 2004), requiring post-hoc manipulations to produce a better home range coverage fit.

A newly developed home range estimator, k nearest-neighbour convex-hull (k-NNCH; Getz & Wilmers, 2004), allows the user to accommodate known areas of non-use with distinct boundaries (*e.g.* cliffs, rivers, lakes, *etc.*) through adjustment of the number of nearest neighbours. Furthermore, the k-NNCH model is easily implemented, constructs better density estimates for the UD and converges on the true home range as sample size increases, unlike the kernel methods (Getz & Wilmers, 2004).

The k-NNCH method involves the construction of convex hulls associated with each point and its (k-1) nearest neighbours. The hulls are then merged and the union of these is taken from the smallest upwards until x% of points are included in the construction of the density isopleths (see Getz & Wilmers, 2004 for details). As a result, areas of zero point density are clearly delineated and form holes in the home range coverage.

In the present study, we use African buffalo (*Syncerus caffer*) dry season locational data that were collected during an on-going study (November 2000-present) of bovine tuberculosis in Kruger National Park. From this data, we first describe the vegetation types selected for by *S. caffer*, through comparisons of proportional use: proportional habitat availability (Neu, Byers & Peek, 1974; in Krebs, 1999). Secondly, we apply the k-NNCH model to delineate high-use and non-use habitat patches for comparisons, thereby investigating the utility of this method in determining ecologically meaningful coverage. Comparisons are based on the dry season abundance of upland grasses and the availability of water from natural sources. Fixed kernel and MCP home range coverage were generated for qualitative comparison.

METHODS

Study Area

This study was conducted in the central region of Kruger National Park (KNP), South Africa. The KNP (ca. 20 000 km²) is situated between 22° 31' S and 25° 31' S, 30° 45' E and

32° 00' E and lies entirely within Universal Transverse Mercator (UTM) Zone 36S. Bordered in the north by the Olifants River and the Sabie River in the south, the central region is divided into two dominant geological substrates along a north/south axis with basaltic and granitic derived soils found on the eastern and western side of the divide, respectively (Gertenbach, 1983; Venter, 1990, Fig. 1a). The influence of fire, wind and rain on the differing parent material has resulted in a complex mosaic of soil types and stream densities that supports a diverse biotic assemblage (Venter, Scholes & Eckhardt, 2003). Based on a combination of landscape (Gertenbach, 1983) and land system (Venter, 1990) classifications, 10 vegetation types were identified within the central region, which include: 1) Knob thorn/Large marula thorn veld (*Acacia nigrescens/Sclerocarya birrea*), 2) Euphorbia/Combretum mountain bushveld, 3) Mopane shrub savanna, 4) Mixed combretum bush savanna, 5) Knob thorn/Albizia thorn thickets, 6) Knob thorn/Marula tree savanna, 7) Dwarf knob thorn savanna, 8) Combretum/Knob thorn rugged veld, 9) Knob thorn/Dichrostachys thorn thickets and 10) Mixed combretum/mopane bush savanna (Fig. 2).

At small scales, stream density on the granitic western side is much greater than that of the basaltic plains due to the differing solubilities of the constituent minerals (Gaylard, Owen-Smith & Redfern, 2003) (Fig. 1b,c). Both the temporal and spatial variability of surface water availability is the result of the interaction of rainfall, evaporation rates and geology (Gaylard *et al.*, in prep; in Gaylard *et al.*, 2003). The rainfall data for 2001-2003 from the Satara rain station show the onset of the dry season, April to September (mean= 6.9 mm, SD= 12.8), and the wet season, October to March (mean= 56.3 mm, SD= 67.0). (Fig. 3)

Telemetry

Radiolocations were collected during an ongoing study of bovine tuberculosis in the Satara Region of the Kruger National Park from November 2000 to July 2004. The number

of radiocollars in-circulation increased each intervening year to the present, where approximately 90 radiocollars are in-and-out of circulation at any given moment. The majority of study individuals were fitted with radio-collars in four helicopter sessions: November 2000 (N = 6), April 2001 (N = 27), August (N = 51) and November 2001 (N = 12). The remaining individuals were darted from ground vehicles throughout the study period. Collared individuals were radio-tracked from a land vehicle or on-foot until visual or auditory contact was made. If an individual was missing for over one month we located it from aircraft. Using a hand-held GPS (UTM WGS84 datum) and laser range finder, the coordinates for the centre of the herds were calculated and recorded. At the time of this study, the study population comprised approximately 1500 buffalo, which represents an estimated 50% of the region-wide population. The number of herds within the study region varied throughout the study period from 4-20, depending upon the degree of herd fragmentation. Although, this fission-fusion nature of the herds may complicate their identification, effective radio-coverage is enhanced as a collared individual immigrates into a previously unidentified group (pers. obs.).

Databases

Dry season locational data (April-September, 2001-2003; April-June, 2004; 417 tracking days) were selected for further processing. From these point locations (N=1447), the five percent harmonic mean outliers were removed to eliminate long-distance dispersal events of certain herds, particularly bachelor groups. Additionally, all remaining point locations lying outside the borders of KNP in adjacent game reserves were also removed (N=9) due to the lack of compatible GIS data. As further removal of point data through concerns of serial independence may reduce the biological relevance of analyses (Blundell, Maier & Debevec, 2001; De Solla, Bonduriansky and Brooks, 1999; Reynolds & Laundre, 1990; Rooney, Wolfe & Hayden, 1998), the remaining point locations (N=1366) were used to form

the basis of the analyses below. Analyses were conducted on buffalo herd positional data, rather than individuals because buffalo were seldom seen alone (*sensu* Hass, 2002). Moreover, evidence suggests that herd daily movements are determined by consensus and not by a single individual (Prins, 1996), thereby obviating between-individual range-use variation. As individual herds were not identified, our study follows a Design I-type study design (Thomas & Taylor, 1990). All shapefiles and data layers used in analyses were obtained from the KNP Geographic Information Systems (GIS) Department. GIS analyses were conducted with ArcView 3.3© software (Environmental Systems Research Institute, 1999) using the UTM WGS84 datum, unless otherwise specified. All locational data manipulations and calculations of home ranges were performed using the Animal Movement Extension© (Hooge & Eichenlaub, 1997) for ArcView 3.3©. (See Appendix for data summary)

Habitat Selection

The Neu method (Neu *et al.*, 1974; in Krebs, 1999) was used to calculate habitat selection indices then standardised (Manly, McDonald & Thomas, 1993; in Krebs, 1999) for between study comparisons. Following this method, the proportion of point locations found within a given habitat type are compared to the proportional availability of that habitat type. Critics of the Neu method have focused on the potential statistical invalidity of using proportional data in analyses (*i.e.* unit-sum constraint) (Aitchison, 1985; in McClean, Rumble, King & Baker, 1998), however, controversy exists over the effectiveness (Tangri & Wright, 1993; in McClean *et al.*, 1998) of the log-ratio transformation employed in compositional analysis to rectify this problem (Aebischer, Robertson & Kenward, 1993). Furthermore, the Neu method was shown to produce more accurate results than compositional analysis techniques when applied to animals of known habitat requirements (McClean *et al.*, 1998)

Proportional use: availability was assessed using a GIS. Herd locational data were plotted onto the vegetation types shapefile, and the minimum convex polygon (MCP; Mohr, 1947) generated. The MCP (*sensu* Ratcliffe & Crowe, 2001) was used to delimit the extent of the study area to minimise type II error caused by the inclusion of peripheral habitats that may truly be unavailable due to external factors (*e.g.* intra/interspecific competition, topography, *etc.*) (Johnson, 1980; McClean *et al.*, 1998). Using the Spatial Analyst extension of ArcGIS 8.3© (Environmental Systems Research Institute, 2000), the vegetation types and MCP shapefiles were converted to raster (100m resolution), the region of intersection between the two layers excised and converted back to shapefile format. In ArcView©, area values for each vegetation type were calculated to determine proportional resource availability. Selection of point data intersecting vegetation types allowed for the calculation of proportional use. Proportional availability for vegetation types that were available yet non-utilised were recorded as 0.001. Moreover, areas non-utilised due to inaccessibility (*i.e.* fenced boma and Satara tourist camp, ca. 8.04 km²) were subtracted from the appropriate vegetation type. A modified chi-square test, G-test, (Manly *et al.*, 1993 in Krebs, 1999) was used to test if use:availability differed from random; Bonferroni modification of the Z statistic allowed calculation of the 95% confidence intervals.

Patch selection

Home ranges for the pooled herd data were calculated using the MCP (Mohr, 1947), fixed-kernel method (Worton, 1989) and the k-NNCH estimator (Getz & Wilmers, 2004). We investigated, specifically, the utility of the k-NNCH method in providing a higher-resolution depiction of within-range space-use than the more traditional MCP and kernel methods. A fixed-kernel home range coverage with a least-squares cross-validated smoothing constant (see Seaman & Powell, 1996) was generated for comparison. Following the minimum covering of spurious holes rule, (Getz and Wilmers (2004), we determined the

number of nearest-neighbours (k) by plotting the area of the k -NNCH coverage, implemented by ArcView© extension, as a function of the MCP area (% MCP) *versus* the k -values. The k -value at the point where exponential growth in the home range coverage faltered, $k=19$, was selected for further analyses (Fig. 4).

Based on the k -NNCH ($k=19$) coverage, shapefiles were created to delineate core-area and “avoided” area polygons. Following convention, core areas were defined as the $>50\%$ density isopleths from the utilisation distribution ($N = 10$; range = 3.25-33.69 km², mean = 11.76 km², total area = 117.64 km²). Areas of zero point density are identified as lacunae because absolute avoidance of the habitat cannot be proven due to the temporal resolution of the data. To optimise between patch differences, the largest 10 out of 15 lacunae patches that were nearest core-use patches were selected ($N = 10$; range = 0.86-21.65 km², mean = 6.76 km², total area = 67.59 km²).

Random points were generated within the core-use and lacunae polygons using the Random Point Generator© extension (Jeness, 2004). Points served as sub-sampling sites, or relevees, for the vegetation characterisation of the habitat patches represented by the polygons. The number of random points assigned per patch corresponded to its areal representation—1 point/ km² for patches of 1-10 km² and 1 point/ 2km² for patches >10 km².

All random points that fell within a burned area/riparian zone/road were relocated 50m beyond the burn front/riparian zone/road. In the cases where the burn front was beyond the visual horizon, another random point was selected.

Vegetation Surveys

In September 2004, vegetation surveys were conducted on the core-use and lacunae patches. Grass surveys were conducted using the Plant Number Scale method (PNS) (Westfall and Panagos, 1988). The Plant Number Scale (Westfall & Panagos, 1988; Westfall, Van Staden & Panagos, 1996) method of determining plant canopy cover is a cover sampling

method based on mean crown diameter and mean crown to crown spacing, derived from Edwards (1983) crown to gap ratios. The mean crown diameter determines cover-sampling transect length while the transect width is based on 4/5ths of the mean crown to crown gap. The number of individuals are counted within the transect and the percentage cover is read off a scale, according to the count. Thus, both plant spacing and aerial size are taken into account in the cover sample. Scale increments are whole plants, resulting in a 33 class scale. Disadvantages of the method include reduced precision because of the classes used for crown diameters, as well as, sometimes insufficient variation being included within transects, especially short transects. A further disadvantage is the difficulty in determining mean crown to crown gap for plants with varied spacing. Spacing can vary considerably for plants with a given cover and density in terms of individuals per hectare. Advantages of the PNS method include: originally developed in South African savannas, elimination of much of the subjective component of other vegetation assessments (*e.g.* Braun-Blanquet, 1928, 1951) and provision of species-specific phytomass, density, spacing and canopy cover estimates via the use of Phytotab-PC (Westfall, 1997)(Westfall, 1998).

As recommended by Westfall *et al.* (1996), 200m² (10m x 20m) quadrats were staked with their northeastern corner at each of the random points. Grasses within the quadrats were identified to species, with crown canopy cover and inter-tuft distances measured. Variable-length belt transects were walked for each species of grass as the number of individuals for each species was counted. Dimensions of the belt transect correlate to the measured crown canopy and inter-tuft distance for each species. Data on the number of individuals counted per species and crown cover classifications were entered into the linear regression model (Westfall, 1987) to produce species-specific phytomass estimates. Phytomass estimates were summed according to species across all relevés within a patch and divided by the total number of relevés per patch to produce species-specific phytomass averages per patch.

Along a transect aligned to optimise within-relevee variation, leaf heights were recorded at 10 points using a measuring rod marked at five centimetre intervals, where the highest leaf touching the rod was recorded. Mean grass-leaf heights were calculated for each patch.

Identified grass species were assigned to one of four categories according to preference from least-preferred (Index-1) to most-preferred (Index 4) (see Table 1). Preference indices were based upon a qualitative assessment of the relative palatability and leaf:stem ratios (see Van Oudtshoorn, 1992) for each species of grass. The categories assigned to each species are generally supported by previous dietary studies of the same herds studied here (J.Bowers, August 2004, unpublished data; Macandza, Owen-Smith & Cross, in press), other studies within South Africa (Page & Walker, 1978; Funston, Skinner & Dott, 1994) and across Africa (Sinclair & Gwynne, 1972; Leuthold, 1972; Vesey-Fitzgerald, 1974; Field, 1976).

Indices of water availability were calculated for the Olifants, Nwasitsontso and Nwanetsi rivers, whose drainage basins intersect the core-use and lacunae habitat patches. The drainage layer files for each river are sub-divided into four river classes, where classes four to one represent a gradient of ephemeral to perennial watercourses, respectively (KNP, GIS). The most ephemeral of the drainage courses, class 4, were eliminated from the analyses because of their disappearance early in the dry season (pers. obs.). River length for the remaining river classes, within the core-use and lacunae patches, was measured using the ArcView© measuring tool. The lengths were summed across river classes for each patch and standardised by dividing by the patch area. Artificial dams and waterpoints were not included, here, because at the scale of our analyses they appeared to have no influence on buffalo herd movements.

Data Analyses

Random-effects, hierarchical analysis using a two-level nested ANOVA was performed on the above environmental variables—preference indices 1-4, mean grass leaf height and the river density index (RDI)—where both levels *A* and *B* are random. Measured variables were nested-in core-use and lacunae patches (*B*), in turn, nested-in geological types (*A*). We log transformed the preference and river density indices to conform to assumptions of normality and homoscedasticity, $\log(\text{Indx}+10)$ and $\log(\text{RDI}+1)$. All statistical analyses were conducted in the Statistica 6 (StatSoft Inc., 2001) software package.

RESULTS

Habitat selection

Within the study region, delimited by the MCP (2896.87 km²), nine out of the ten region-wide vegetation types were represented: mixed bushwillow/mopane bush savanna (1.7%), Mopane shrub savanna (2.5%), bushwillow/knob thorn rugged veld (11.1%), knob thorn/marula tree savanna (32.7%), dwarf knob thorn savanna (11.8%), mixed bushwillow bush savanna (18.5%), knob thorn/large marula thorn veld (0.8%), euphorbia/bushwillow mountain bushveld (5.4%), knob thorn/false-thorn thorn thickets (15.4%). Results of the G-test indicated use of these habitats by *S. caffer* significantly differed from random ($\chi^2=516.84$, $df=8$, $p<0.0001$). Comparisons of proportional-availability to the 95% confidence intervals (Bonferroni corrected $Z=2.77$, two-tailed, $p=0.05/9=0.0056$) of proportional-use showed selection for dwarf knob thorn savanna and knob thorn/marula tree savanna vegetation types. Standardised selection indices for the former and latter vegetation types are 0.292 and 0.284, respectively (see Table 2 for summary).

Patch selection

Home ranges for pooled herd data ($N=1366$) were calculated following the MCP (2896.87 km²), the fixed kernel method (928.11 km², $h=LSCV$) and the k-NNCH method (2125.12 km², $k=19$) (Figs. 5a,b). A nested ANOVA general linear model was used to test

the ecological relevance of the habitat patches delineated by the k-NNCH method based on six variables of resource abundance—an index of water availability (RDI) and four indices of grasses (see Figs. 6a,b for data summary).

Planned, multivariate comparisons of least squares means (Wilk's lambda) for level A groups, geology type, found no overall significant difference between the measured environmental variables ($F = 2.010$, effect $df = 6$, error $df = 11$, $p = 0.149$), however, the contrast estimate for $\log(\text{RDI}+1)$ significantly differed between geology types ($t = -2.310$, $p = 0.035$). Results of planned comparisons for the sub-groups, patch-use, indicated that core-use and lacunae patches significantly differed ($F = 4.927$, effect $df = 6$, error $df = 11$, $p = 0.011$), where contrast estimates for the $\log(\text{RDI}+1)$ and $\log(\text{Ind3}+10)$ variables were the predominant contributors ($t = -5.362$, $p < 0.001$ and $t = -3.070$, $p = 0.007$, respectively) (see Tables 3a, b, c for summary of planned comparisons).

From the test of the whole model sum of squares (SS) *versus* residual SS, the $\log(\text{RDI}+1)$ and $\log(\text{Ind3}+10)$ variables were significant ($F = 13.4976$, model $df = 3$, $p < 0.001$; $F = 5.3429$, model $df = 3$, $p = 0.01$, respectively). The adjusted coefficient of determination, R^2 , for the two significant variables in the model, $\log(\text{RDI}+1)$ and $\log(\text{Ind3}+10)$, are 0.664 and 0.407, respectively (Table 4). Equations from the model for these significant variables follow:

$$\log(\mathbf{RDI}+1) = 0.950660915 - 0.79198225 * \text{"Patch-use"}(\text{Geology}) - 0.77081973 * \text{"Patch-use"}(\text{Geology}) - 0.53951109 * \text{"Patch-use"}(\text{Geology})$$

$$\log(\mathbf{ind3}+10) = 2.17627598 - 0.08692017 * \text{"Patch-use"}(\text{Geology}) - 0.66016221 * \text{"Patch-use"}(\text{Geology}) + 0.017363494 * \text{"Patch-use"}(\text{Geology})$$

Results of post-hoc comparisons, Tukey's Unequal-N HSD, of the nested combinations (*e.g.* lacunae/granite, lacunae/basalt, core-use/granite and core-use/basalt) show that for the log(RDI+1) core-use/basalt significantly differed from both lacunae/basalt and lacunae/granite (df = 16, $p < 0.001$ and $p = 0.006$, respectively). Nested comparisons for grass preference index-3, resulted in significance between core-use/basalt and lacunae/basalt (df = 16, $p = 0.012$

DISCUSSION

Habitat selection

At the landscape level, our results of habitat selection by buffalo concur with previous South African studies, in that, open grasslands and bushveld habitats are generally preferred (Ryan, Knechtel & Getz, in press; Funston *et al.*, 1994). In our study these general habitat types are represented by the Knob thorn/Marula tree savanna (KTMS) and Dwarf knob thorn savanna (DKTS) vegetation types, following the KNP classification system. The KTMS vegetation type is an open, *Acacia nigrescens/Sclerocarya birrea* savanna, where the DKTS is a dense to open, *Acacia nigrescens/Cordia ovalis/Acacia borleae* bush savanna (for detailed description see Venter, 1990).

Selection indices for DKTS and KTMS vegetation types (1.607 and 1.571, respectively) were not significantly different ($\chi^2 = 0.20$, df = 1, $p > 0.5$). The equal preference of buffalo for open and bush savanna seems counter-intuitive, as they are largely considered bulk grazers (Estes, 1991). Previous studies have shown, however, that consumption of woody vegetation may fluctuate seasonally (Sinclair, 1972) and often increases as the dry season progresses (Stark, 1986). Moreover, a recent survey of the literature found that the average intake of dicots by buffalo is as great as 22.5% (Gagnon & Chew, 2000), yet as little as 1.9% has also been observed (Prins, 1996).

In addition to supplying potential browse, the bushveld system may also act as a dry-season reserve for the highly palatable grass species, *Panicum maximum*. Preferred by most herbivores, *P. maximum* in more open habitats is likely to be one of the first grass species to be depleted as the dry season progresses. However, this species' tendency to grow at the bases of shrubs and trees, where it's usually heavily defended by thorns, may provide it protection from grazing pressures (pers. obs.). This phenomenon was, similarly, observed at Hluhluwe Game Reserve (Page & Walker, 1978). In explanation, the authors described how the buffalo use their bosses to push the small trees and shrubs away in order to capitalize on these palatable grass reserves.

Patch selection

From our patch selection analyses, 3rd order selection (Johnson, 1980), we found that the preference index-3 and the river density index (RDI) significantly differed between core-use and lacunae patches. A post-hoc comparison of these variables revealed that the model's overall level of significance was heavily influenced by the differences between the core-use and lacunae patches on the basaltic side. These one-sided differences are likely due to the low statistical power of the granitic-side comparisons (N=3 versus basaltic N=7), as a similar increase for both of these variables in the core-use/granitic patches was also observed (see Figs. 6a,b).

The ecological implication of the RDI as a significant contributor to our model may be relatively straightforward, as the water dependence of buffalo is well documented (Prins, 1996; Gaylard *et al.*, 2003). However, it should be noted that an interaction likely exists between river density and riverine vegetation, where watercourses that retain water throughout the dry season will likely be a source of succulent grasses, such as *Panicum deustum* (*sensu* Sinclair, 1977). Therefore, water availability *per se* may not be the sole

motivator when considering natural water sources as a selection factor. In our study, only upland grasses were considered, thus, no definitive conclusions are reached in this regard.

Our analyses of grass preference indices 4-2 illustrate that the abundance of the most-preferred species varies little between substrates and patch treatments, whereas for indices-2 and 3 greater abundances are found within core-use patches with index-3 significantly differing. These findings are supported by the extensive studies of the buffalo of Lake Manyara, Tanzania (Prins, 1996). Through nutritional analyses of grazed grass species, Prins (1996) found that buffalo don't necessarily select the most nutritious grass species available, which would maximise their crude protein intake. Due to the physiology of ruminant digestion, too high a protein intake may result in pathology (*i.e.* acidosis). Thus, the selection of graze requires a balancing of crude protein: fiber intake. From the species composition of index-3 grasses, it appears that *Setaria spp.* (*S. incrassate* and *S. nigirostris*) and *Ischaemum afrum* may play a pivotal role in this nutritional balance and, therefore, the selection of patches by our study population (Fig. 7).

Interestingly, the trend in our data for index-1 follows expectations, in that, the least palatable grass species appear to be avoided, as their abundances decrease within the core-use patches. Other forage selection studies of the same buffalo population have shown, however, that at 4th and 5th order scales (Johnson, 1980) index-1 species are consumed in limited to moderate amounts, particularly *Bothriochloa spp.* (*B. radicans* and *B. insculpta*) (Macandza *et al.*, in press; J.Bowers, August 2004, unpublished data). Such findings illustrate the scale-dependent nature of forage selection research (Johnson, 1980; Kotliar & Wiens, 1990).

The observed non-significant increase of the mean grass leaf height within the core-use patches is similar to previous studies that found buffalo seemingly prefer taller grass (Page & Walker, 1978; Prins, 1996; Perrin & Brereton-Stiles, 1999). As in other regions of Africa, male lions are the main predator of adult buffalo (Funston, 1999), thus their

preference for tall grass seems counter-intuitive from a predator avoidance perspective. Nonetheless, the long-term studies of the Lake Manyaran buffalo conclude, in regards to patch selection, “Buffalo ignore predation risk when deciding where to graze.” (Prins, 1996). Consequently, patch selection appears to be a resource-driven phenomenon, albeit further research is needed.

A final trend worth noting from our data is the differences in the variation of the measured variables between the granite and basalt substrates and, to a lesser extent, between the core-use and lacunae patches. Logically, it follows that the less reliable is the occurrence and abundance of vital resources, the smaller the population of a given species the resources may support. From our data this is evidenced by the presence of two utilisation foci, or cores, on the nutrient-rich, basaltic substrate compared to the one less prominent core area on the granitic substrate. The effects of this resource variation on the resident buffalo population(s) may then be compounded through increased inter-specific competition, as a consequence of the uneven distribution of resources (Doncaster, 2001).

As a matter of comparison to the k-NNCH method, home range estimates from the traditional MCP and fixed-kernel were calculated. The k-NNCH method produced estimates intermediate to the MCP and kernel methods. Due to the heavy influence of outliers, the MCP coverage is the least ecologically meaningful of the three models compared here. Although the kernel estimate is more conservative than that of the k-NNCH method, the fragmented coverage produced by the kernel is certainly spurious. The small “islands” of coverage make little ecological sense, as the herds are known to be panmictic with no barriers to their movements (see Figs. 5a,b).

CONCLUSION

The results of our nested analyses indicate that the areas delineated by the k-NNCH method are, indeed, ecologically relevant and not just an artefact of the construct. Thus, we provide supportive evidence for the utility of the k-NNCH home range estimator in producing a greater resolution depiction of within-range space-use beyond that of a blanket utilisation distribution function. Furthermore, through comparisons with traditional home range estimators, the k-NNCH method produced a coverage intermediate in extent, yet seemingly ecologically meaningful. Future research in this field should be directed towards investigations of the response of the k-NNCH construct to other animal models, the affect of dataset size and k-level manipulations on the delineation of ecologically relevant patches and its associated typeI/typeII error rate trade-offs.

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Appendix

Month	Year				Total
	2001	2002	2003	2004	
4	121	59	71	51	302
5	92	66	34	56	248
6	88	64	64	46	262
7	40	72	71	0	183
8	85	53	66	0	204
9	60	55	52	0	167
Total	486	369	358	153	1366

Appendix 1. Temporal distribution of buffalo locational data

Table 1. Assigned preference indices for identified species of grass

least preferred			most preferred
1	2	3	4
<i>Cymbopogon plurinodis</i>	<i>Eragrostis spp</i>	<i>Schmidtia pappophoroides</i>	<i>Cenchrus ciliaris</i>
<i>Aristida spp</i>	<i>Tricholaena monachne</i>	<i>Setaria spp</i>	<i>Panicum spp</i>
<i>Bothriochloa spp.</i>	<i>Melinis repens</i>	<i>Heteropogon contortus</i>	<i>Themeda triandra</i>
<i>Pogonarthria squarrosa</i>	<i>Enneapogon spp</i>	<i>Fingerhuthia africana</i>	<i>Urochloa spp</i>
<i>Perotis patens</i>	<i>Sporobolus spp</i>	<i>Brachiaria spp</i>	<i>Digitaria eriantha</i>
	<i>Chloris spp</i>	<i>Ishaemum afrum</i>	
	<i>Alloteropsis semialata</i>	<i>Dactyloctenium australe</i>	
		<i>Enteropogon monostchys</i>	

Comparison	Test	Value	F	Effect	Error	p
				df	df	
Geology (A)	Wilks	0.477	2.010	6	11	0.149
Patch-use (B)	Wilks	0.271	4.927	6	11	0.011

Table 3a. Planned comparisons of nested levels A and B

Table 3b. Contrast estimates from level *A* planned comparisons

Variable	Estimate	Std. Err	t	p	Lwr 95% Cnf Lmt	Uppr 95% Cnf Lmt
Grass Ht	-5.585	14.460	-0.386	0.704	-36.239	25.068
log(RDI+1)	-1.794	0.335	-5.362	0.000	-2.503	-1.085
log(Ind1+10)	0.585	0.575	1.018	0.324	-0.634	1.805
log(Ind2+10)	-0.445	0.541	-0.821	0.424	-1.592	0.703
Variable	Estimate	Std. Err	t	p	Lwr 95% Cnf Lmt	Uppr 95% Cnf Lmt
Grass Ht	3.728	5.245	0.711	0.488	-7.392	14.847
log(RDI+1)	-0.280	0.121	-2.310	0.035	-0.538	-0.023
log(Ind1+10)	0.275	0.209	1.316	0.207	-0.168	0.717
log(Ind2+10)	-0.054	0.196	-0.274	0.788	-0.470	0.363
log(Ind3+10)	0.295	0.168	1.754	0.099	-0.062	0.652
log(Ind4+10)	0.081	0.065	1.245	0.231	-0.057	0.218
log(Ind3+10)	-1.425	0.464	-3.070	0.007	-2.408	-0.441
log(Ind4+10)	-0.074	0.179	-0.413	0.685	-0.453	0.305

Table 3c. Contrast estimates from level *B* planned comparisons

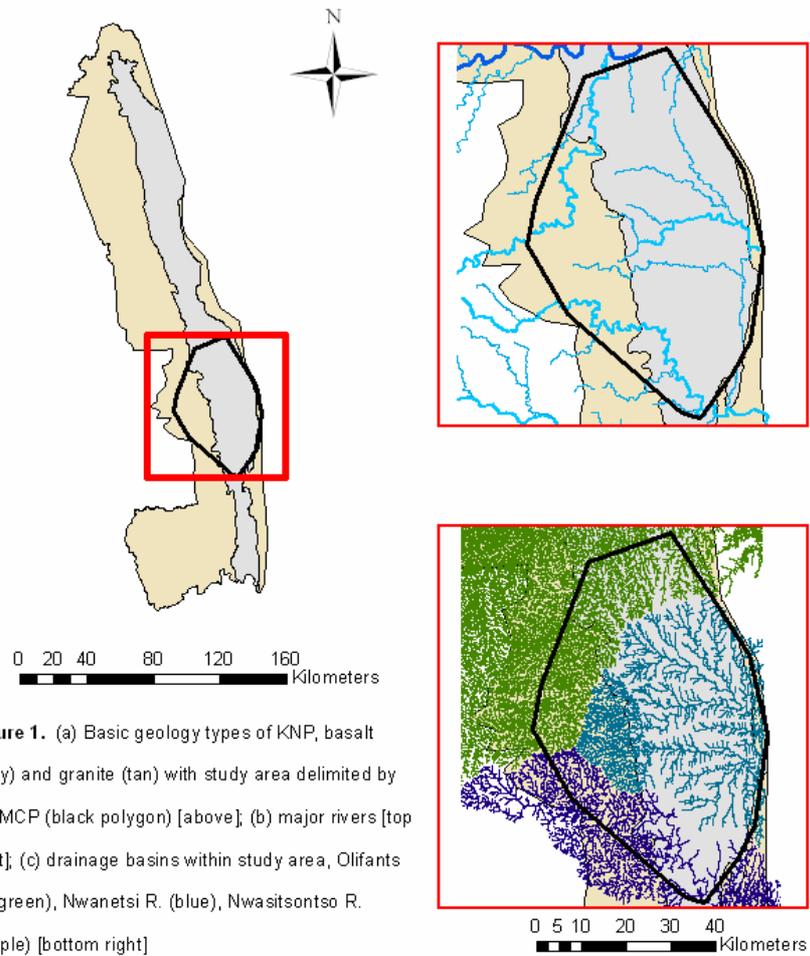


Figure 1. (a) Basic geology types of KNP, basalt (grey) and granite (tan) with study area delimited by the MCP (black polygon) [above]; (b) major rivers [top right]; (c) drainage basins within study area, Olifants R. (green), Nwanetsi R. (blue), Nwasitsontso R. (purple) [bottom right]

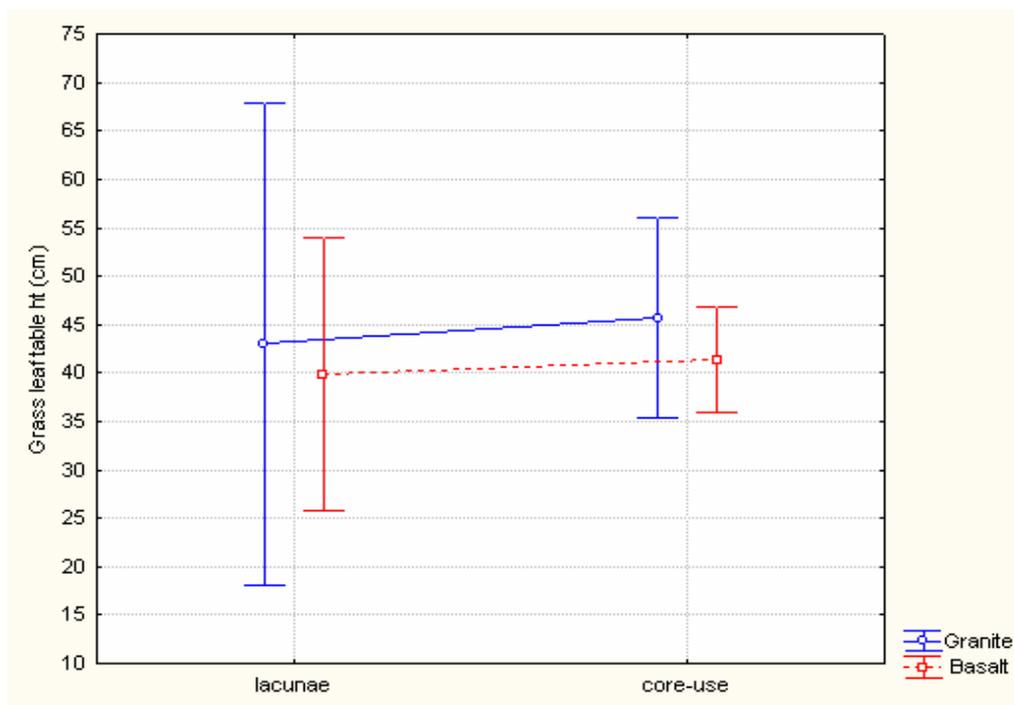
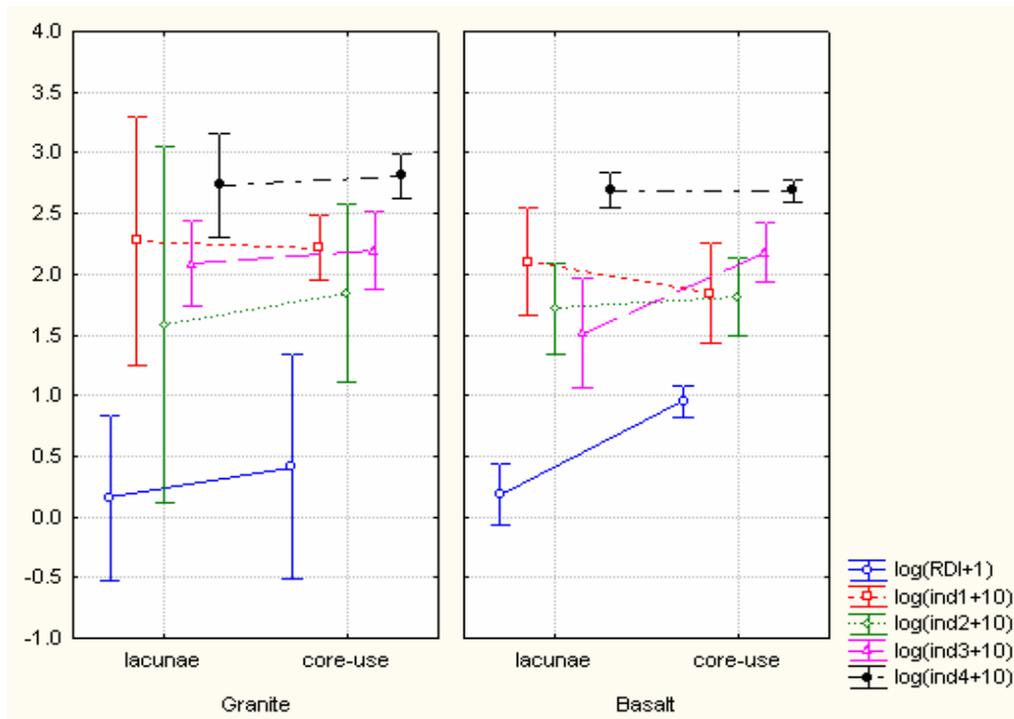


Figure 6a. “Patch-use”(Geology) nested, weighted means; vertical bar denotes 0.95 confidence interval

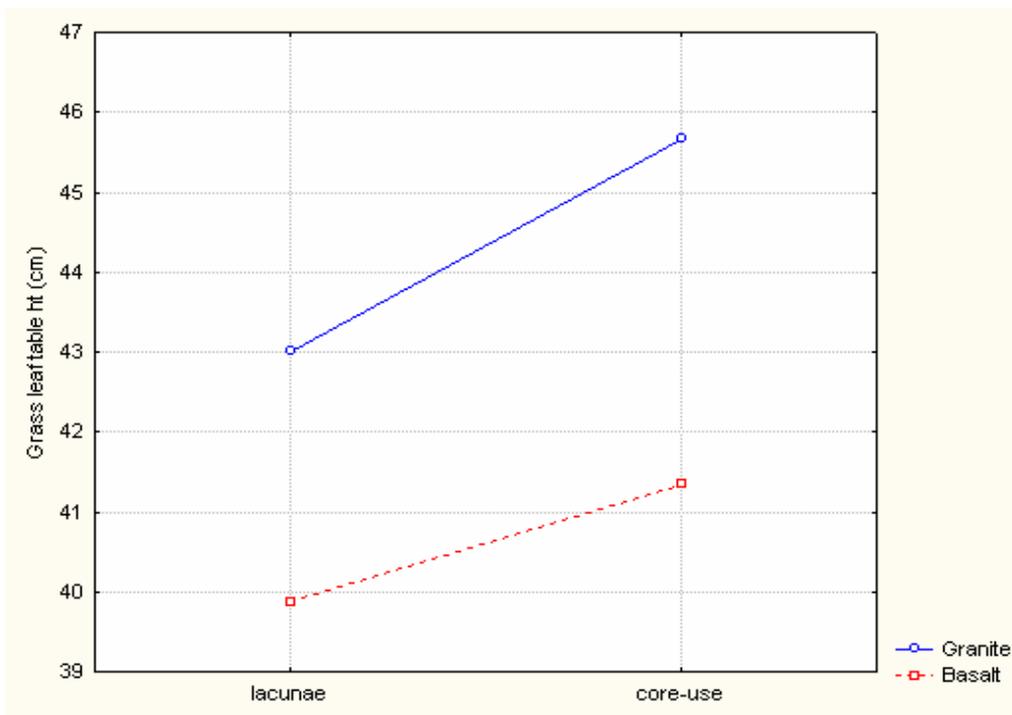
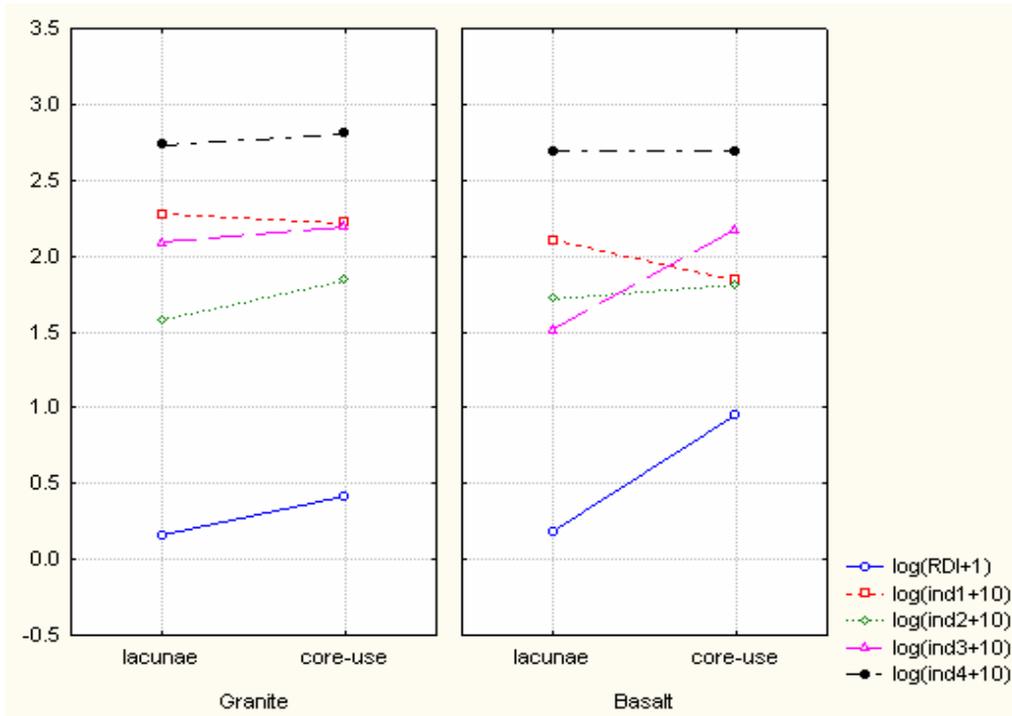


Figure 6b. “Patch-use”(Geology) nested, least squares means

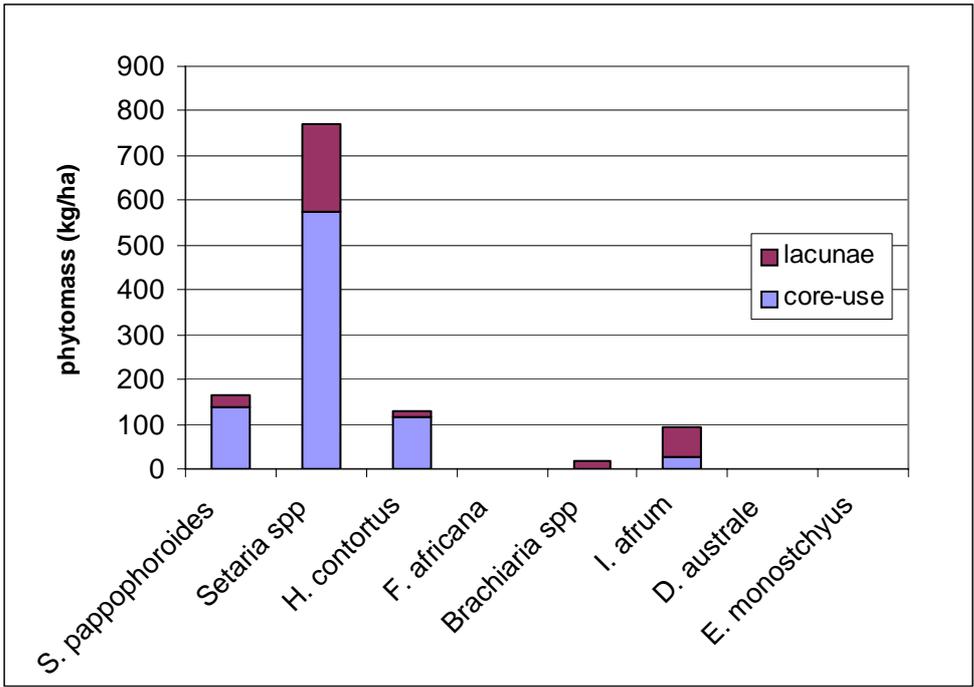
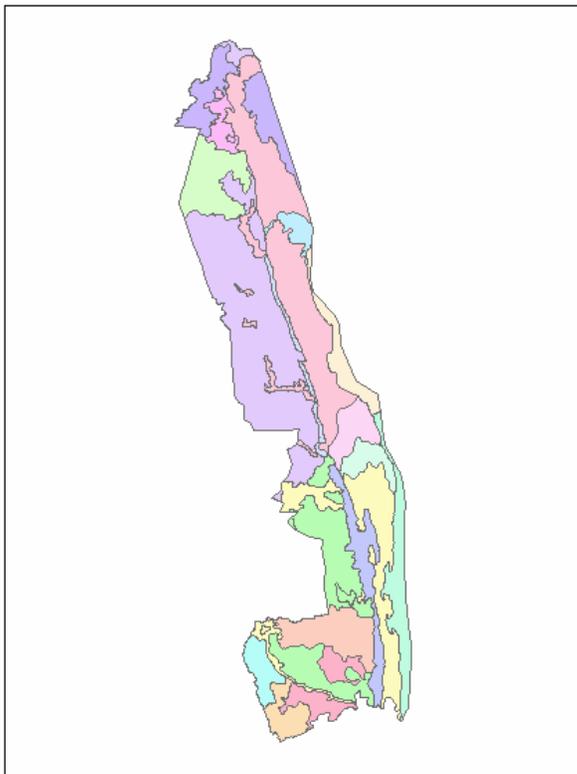


Figure 7. Preference index-3 species composition and abundance for core-use and lacunae habitat patches



Vegetation Classification

- Combretum/Euclea Bushveld
- Combretum/Knob Thorn Rugged Veld
- Combretum/Mopane Rugged Veld
- Dwarf Knob thorn Savanna
- Euphorbia/Baobab Mountain Bushveld
- Euphorbia/Combretum Mountain Bushveld
- Knob Thorn/Albizia Thorn Thickets
- Knob Thorn/Dichrostachys Thorn Thickets
- Knob Thorn/Large Marula Thorn veld
- Knob thorn/Marula tree Savanna
- Mixed Combretum bush Savanna
- Mixed Combretum/Mopane bush Savanna
- Mixed Combretum/Terminalia Tree Savanna
- Mopane Tree Savanna
- Mopane shrub Savanna
- Mopane/Knob Thorn Savanna
- Sandveld Communities
- Terminalia/Rock Ficus Sour Bushveld

Figure 2. Vegetation types of the Kruger National Park (KNP, GIS)

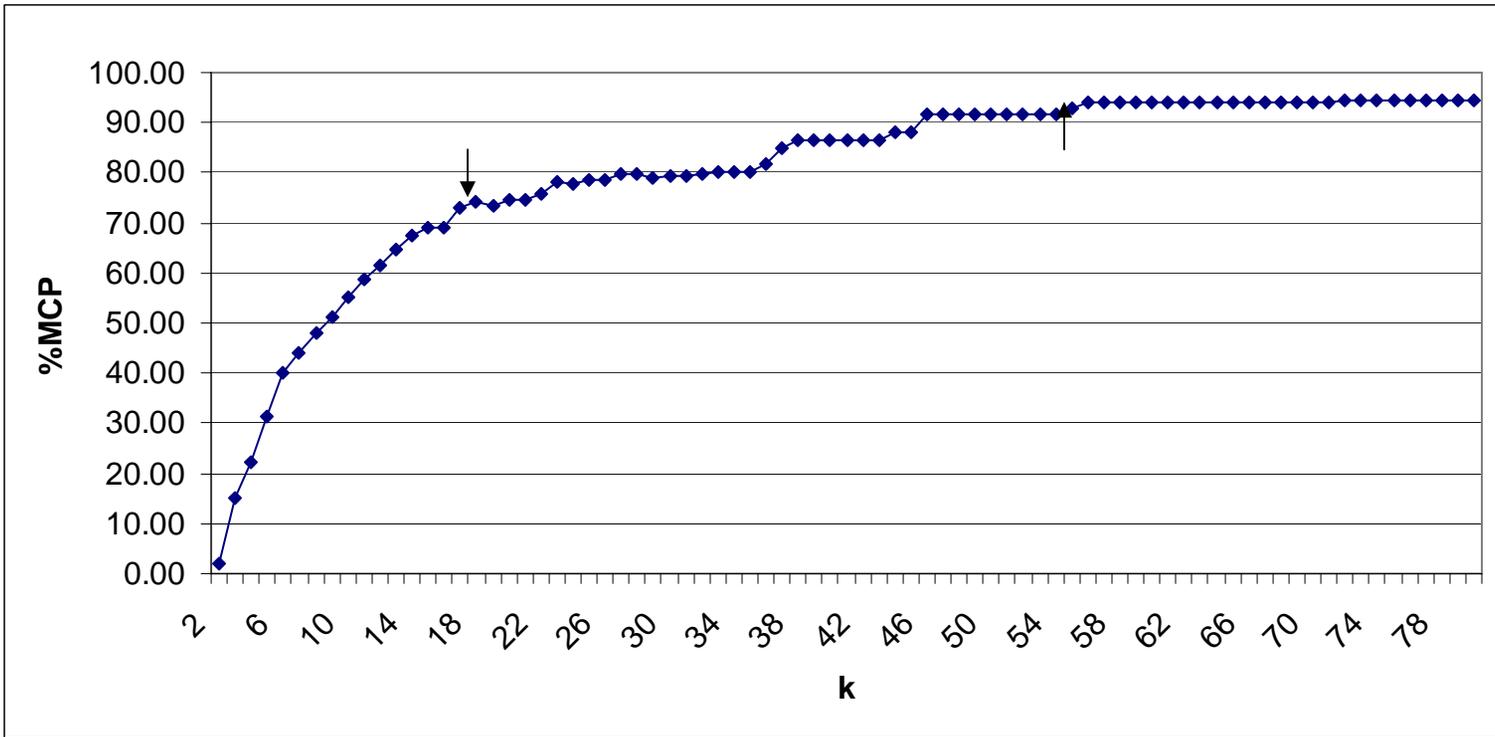


Figure 4. Growth (%MCP) of the k-NNCH home range coverage as the k-value increases; arrows mark k= 19 and k= 56

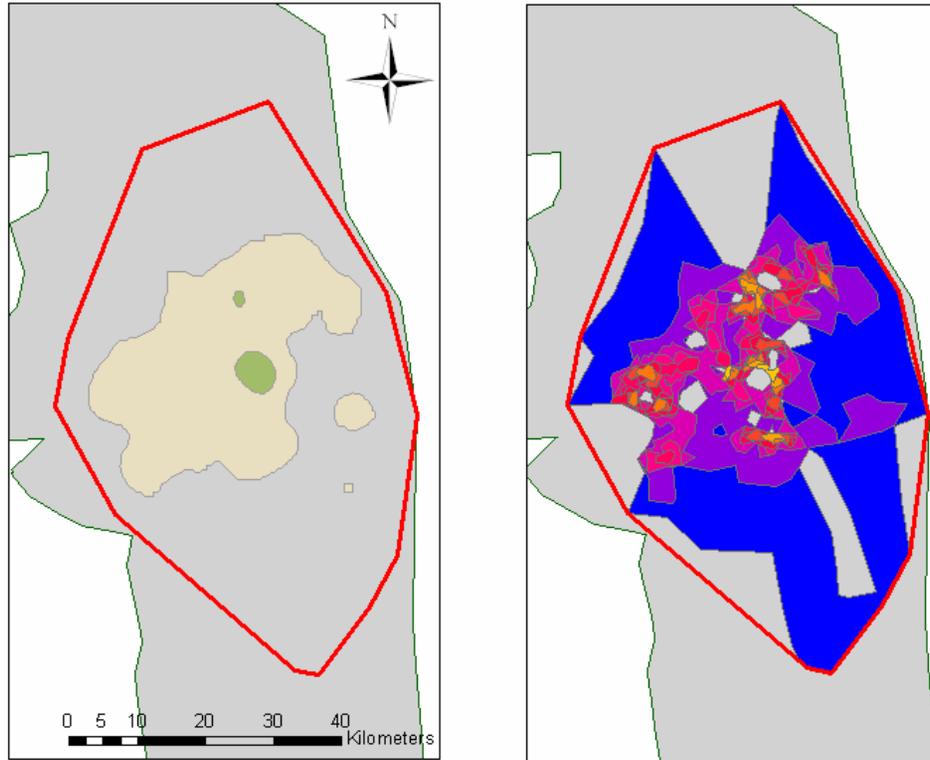


Figure 5. (a) fixed kernel home range coverage, 50% point density (green) and 95% (tan);
(b) k-NNCH home range coverage, density isopleths colored at 10% intervals

Table 2. Proportional use and availability by vegetation type following the KNP classification system

Vegetation types Variable	Multiple R	Multiple R ²	proportional Adjusted R ² use	95% Confidence Intervals			proportional MS Model availability	SS Residual df Residual ratio (SE)	Standardised MS Residual ratio	F Selection	p	
				SS Model	Lower CI	Upper CI						
Mixed Combretum/Mopane Bush Grass Ht Savanna	0.1998	0.0397	-0.1403 0.0044	76.4509 -0.0006	3	0.0093	25.4836 0.0170	1848.7737 0.258 (0.105)	16 0.047	115.5484	0.2205 (-)	0.8807
<i>log(RDI+1)</i>	0.8466	0.7168	0.6637	2.5053	3	0.8351	0.9899	16	0.0619	13.4976	0.0001	
Mopane Shrub Savanna			0.0029	-0.0011		0.0070	0.0250	0.117 (0.059)	0.021		(-)	
<i>log(ind1+10)</i>	0.4020	0.1616	0.0044	0.5639	3	0.1880	2.9256	16	0.1829	1.0280	0.4065	
Combretum/Knob thorn Rugged Veld			0.0161	0.0067		0.0256	0.1110	0.145 (0.031)	0.026		(-)	
<i>log(ind2+10)</i>	0.2297	0.0528	-0.1249	0.1444	3	0.0481	2.5920	16	0.1620	0.2970	0.8270	
Knob Thorn/Marula Tree Savanna			0.5110	0.3957		0.9067	0.3250	1.572 (0.0416)	0.285		(+)	
<i>log(ind3+10)</i>	0.7074	0.5005	0.4068	1.9079	3	0.6360	1.9045	16	0.1190	5.3429	0.0096	
Dwarf Knob Thorn Savanna			0.1896	0.1602		0.2190	0.1180	1.607 (0.090)	0.292		(+)	
<i>log(ind4+10)</i>	0.3340	0.1115	-0.0550	0.0355	3	0.0118	0.2824	16	0.0176	0.6696	0.5830	
Mixed Combretum Bush Savanna			0.1325	0.1071		0.1579	0.1850	0.716 (0.050)	0.130		(-)	
Knob Thorn/Large Marula Thorn Veld			0.0001	-0.0002		0.0003	0.0080	0.000	0.000		(-)	
Euphorbia/Combretum Mountain Bushveld			0.0139	0.0051		0.0227	0.0540	0.258 (0.059)	0.047		(-)	
Knob Thorn/False-thorn Thorn Thickets			0.1296	0.1044		0.1548	0.1535	0.841 (0.059)	0.153		0	
Total			1.0001				0.9965		1.001			

Table 4. Results of the sum of squares whole model *versus* sum of squares residual test